

BENTHIC COLONIZATION IN FRESH WATER: A SYNTHESIS

MICHAEL J. S. TEVESZ

Department of Geological Sciences
Cleveland State University

Abstract

Colonization of defaunated substrata by benthic organisms proceeds in an orderly and predictable manner in diverse freshwater environments. Early colonizers tend to be relatively small organisms that have broad environmental tolerances and high powers of dispersal. They occur in communities where species richness is low. Later colonizers, by contrast, occur in more diverse communities. They also tend to be larger and possibly better protected.

These findings suggest that the structure and colonization patterns of freshwater communities are linked to environmental factors, the most obvious of which is the temporal proximity to disturbance. The causes of natural disturbances that locally destroy portions of freshwater benthic communities are varied, yet the functional response of those communities to the disturbance is invariably similar. These findings are in contrast to long held views which placed great importance on the controlling influence of ambient physical/chemical environmental parameters. As is also the case in marine ecosystems, it seems that community structure and dynamics in fresh water are closely related to the frequency of disturbance.

Introduction

The factors that control community structure and dynamics in freshwater ecosystems are poorly understood. This is due in part to the diverse array of habitats found in fresh water and to the paucity of taxonomic and autecological information that is available concerning the organisms which inhabit them. Nevertheless, information recently gathered on the structure and dynamics of marine communities may shed light on these heretofore perplexing aspects of freshwater systems.

Studies by McCall (1977) and Rhoads et al. (1978) demonstrated that disturbance initiates an orderly pattern of community recovery that may be called a succession. A low-diversity community appears soon after the disturbance and consists of abundant, patchily distributed organisms (pioneer species). Over a period of a few months to a year, this community is replaced by a more diverse assemblage of organisms. The early stages of this recovery process are characterized by small, often unshelled organisms that live on or close to the sediment-water interface. Later stages are dominated by larger, less numerous organisms that live at greater depths within the sediment or possess some other form of protection from disturbance (e.g., shell, rapid burrowing ability).

Moreover, McCall (1977) demonstrated that shallow-water ($\leq 7\text{m}$) communities inhabiting Long Island Sound were dominated by pioneer species, while deeper water

communities were characterized by later colonizers. Thus the frequency of a single factor—disturbance—dictates general aspects of community structure and dynamics in portions of the marine realm. These findings are in contrast to long held views which placed great importance on the controlling influence of ambient physical/chemical environmental parameters.

In the marine realm, the response of organism communities to disturbance is predictable and general, transcending the taxonomic composition of the communities and the physical and chemical settings in which they occur. In freshwater environments, the response of organism communities to disturbance is not well known, but, judging from the success of marine-based studies, may reveal factors that influence community structure and dynamics.

Researchers studying the role of disturbance in marine communities generally have obtained their information by eliminating a benthic community in a portion of its habitat and then monitoring the recolonization process. This is often accomplished by collecting and defaunating the substratum, replacing it in the environment, and then collecting it again at predetermined intervals.

Similar procedures are used in gathering information in freshwater ecosystems, but often for different purposes. For example, artificial substrate samplers are frequently used to sample the benthos of streams. But the researchers who use them are mainly interested in gathering a taxonomically representative sample of the benthos rather than insights into the colonization process. Much information is also available on the development of faunas in man-made lakes. Nevertheless, the information is often used for purposes such as estimating fish food production rather than trying to better understand benthic community dynamics per se. Information on colonization in fresh water is, moreover, scattered within the literature.

This paper attempts to draw together and reinterpret published information on colonization patterns and processes in diverse freshwater habitats. Particular attention is paid to the taxonomical and functional response of organism communities to disturbance and other physical and chemical parameters that affect the colonization process. It is hoped that this new synthesis will better document the factors controlling the structure and dynamics of freshwater communities. In addition, by evaluating the relationship of freshwater communities to disturbance, information will be presented that may be useful in assess-

ing the abilities of the communities to recover from such man-made disasters as pollution events.

This paper is not intended to be a comprehensive review of colonization in fresh water, even though an extensive published literature is summarized and discussed. Rather, examples of studies from a broad range of freshwater habitats are presented so as to reveal a pattern that may be generally instructive.

COLONIZATION PATTERNS AND PROCESSES

Running Water

Permanent Streams and Canals

Native substrata. Tevesz (1978) reported the results of two consecutive recolonization experiments involving defaunated and deflorated native sediments which were replaced in the Vermilion River, Ohio, during summer months. The numerically dominant macroinvertebrates in the studied portion of the river were immature insects, oligochaetes (annelid worms), gastropods, and bivalves (molluscs). Chironomid (midge fly) larvae were among the first and most abundant colonizers. They appeared in the samples within three days and reached population densities of 525 individuals/m². Oligochaetes, gastropods, and bivalves appeared toward the end of the first week or later, in comparatively low population densities (usually <250/m²).

Every macroinvertebrate taxon sampled from the study area appeared in the colonization sequence by the fifth week in the first study, and by the twenty-fourth day in the second study. Both propensity for drifting (high mobility) and high relative abundance were the most obvious features of the early colonizers. In addition, almost all colonizers were fairly advanced instar stages or adults. Thus summer colonization in the study area was not primarily a reproductive event.

In a similar study done in Valley Creek, Minnesota, Waters (1964) found that the two numerically dominant riffle-inhabiting organisms, *Baetis vagans* (mayfly) and *Gammarus limnaeus* (amphipod), could completely recolonize riffle areas within one to two days. As in the case of the Vermilion River, it was concluded that drift was the mechanism largely responsible for rapid colonization. Similarly, Williams and Hynes (1976) demonstrated that drift was the most important source of colonizing organisms in a Canadian stream, accounting for 41.4% of the total number of sampled organisms. Nevertheless, other sources also contributed to the recolonizing process. Aerial sources, upstream migration, and upward migration from within the substratum contributed 28.2%, 18.2%, and 19.1%, respectively, of the colonizing fauna.

Artificial substrata. The benthos of running waters are difficult to sample by traditional implements such as dredges, corers, and grabs, because lotic sediments are

frequently coarse. Some of the most successful samplers that have been developed to get around this problem employ colonizing activities of the benthos. These artificial substrate samplers may be placed in or on the substratum or suspended above it. They are then collected at predetermined intervals. The samplers are, in effect, abiotic islands of foreign substrata that become colonized by stream-dwelling benthos.

Cover and Harrel (1978) describe in detail the colonization of multiplate samplers by the benthos of a freshwater canal near Orange, Texas. The samplers were made of tempered hardboard and attached to bricks. The bottom plate of the sampler extended into the water 32 cm above the brick. The samplers were removed from the canal each week for 16 weeks. Cover and Harrel's samples revealed that during the first week of the experiment, 283 individuals representing 27 species colonized the samplers. Eighteen of these species were chironomid larvae, but the apparent chironomid dominance declined later in the experiment. By the fifth week of the experiment, gastropods and hydropsychid trichopteran (caddisfly) larvae were well represented on the samplers. The authors attributed this to the increase in algal scum on the samplers. Oligochaetes also increased in number as the amount of sediments trapped by the samplers increased. By the fifth week, various pioneer species (mainly chironomids) were greatly reduced in number or had disappeared entirely. Trichopterans were dominant in number and biomass later in the experiment.

Throughout the experiment, biomass and productivity varied greatly and were strongly affected by the presence or absence of a few large organisms. Also, by week seven, large predators (Odonata: dragonfly nymphs) appeared and affected these properties as well. Neither collection diversity nor cumulative diversity became asymptotic during the study. At the end of the study, 68 of the 102 taxa on the natural bottom were present on the samplers. The numerically dominant organisms on the natural bottom, oligochaetes, were never dominant on the samplers.

The overall taxonomic pattern of colonization revealed by this study is a pioneer assemblage of chironomids that is later replaced by a more diverse assemblage dominated by trichopterans. Cover and Harrel thought that the organisms that colonized the samplers would have to be highly motile forms (e.g., prone to swimming and drifting). They said that chironomids have this characteristic and, moreover, are generally known to be able to inhabit a wide variety of aquatic environments, have wide ecological tolerances, and are thus ideal pioneer species. The authors added that these pioneer organisms rapidly increased in numbers because of the absence of competition in the early stages of recolonization. But later, biotic disturbance (e.g., predation) eliminated both individuals and species. The taxonomic and trophic pattern of colonization also appeared to be influenced by the physical and biotic "conditioning" of the substratum. For example,

gastropods and hydropsychid trichopterans successfully colonized the samplers only after an algal scum (their presumed food source) appeared.

Other studies have also linked substratum conditioning to the colonization process. When Glime and Clemons (1972) compared invertebrate colonization on the plant *Fontinalis* and on string and plastic artificial mosses, they found that organisms readily colonized all three substrates (24 species on *Fontinalis*; 23 species on string "moss"; 13 species on plastic "moss"). Nevertheless, organism abundances were the highest on the edible *Fontinalis*. From this they concluded that colonization by periphyton (a form of substratum conditioning) is a possible determinant of the rate of macrofaunal colonization. They also concluded that the area or volume of the colonized substrate is related to overall organism number. However, they considered the physical nature of the substrate surface to be generally unimportant, presumably as long as it was not related to food availability.

Similarly, Mason et al. (1970) found that worms abundantly colonized basket samplers only after sediment began to accumulate, and that certain mayflies and midges colonized the basket samplers only after algae grew on them.

Intermittent Streams

Temperate regions. Stehr and Branson (1938) and Larimore et al. (1959) provided information on benthic recolonization of stream beds in Ohio and Illinois following seasonal drying. They reported that adult insects survived seasonal drying by flying or crawling to other bodies of water. Then they returned to recolonize the river primarily by oviposition. Molluscs, worms, and certain crustaceans dug into the substratum or nestled in rock crevices (Stehr and Branson 1938). Trichopterans survived in seasonally dry stream beds as aestivating larvae and pupae. Ephemeropterans (mayflies) and plecopterans (stoneflies) survived as small nymphs or eggs. Small crustaceans such as amphipods and isopods survive within the substratum as a result of seepage and water-saturated air space (Clifford 1966).

Larimore et al. (1959) defined a taxonomic pattern of benthic recolonization following a severe drought in Illinois in 1953–54. They reported that their studied stream ran full from early April until early July 1954. In samples taken on April 2, which approximately coincided with the return of full flow, they reported that chironomids occurred in every collection and were the most abundant organisms. By July, chironomids were greatly reduced in number and the benthos was more diverse, with ephemeropterans and crayfish predominating. The following year a similar pattern was evident although the early colonizing chironomids were less abundant, whereas such organisms as gastropods, beetles, caddis larvae, and oligochaetes were more abundant.

Tropical regions. Hynes (1975) studied benthos recolonization in riffle areas of a Ghanan (Africa) stream after a drought. He found that the earliest colonizers were organisms that had survived the drought in pools and then were washed downstream. These included Cladocera, Ostracoda, and Hydracarina (all arthropods). Then, during the first and second weeks of flow, chironomids, *Centroptilum* (baetid mayfly), and *Simulium* (dipterid primary consumer) appeared in large numbers as a result of oviposition. The chironomids subsequently declined in relative importance after the first week, compared to baetid mayflies.

This early succession of invertebrates was paralleled by a succession of primary producers. Immediately after the onset of flow, filamentous green algae, generally present in the stream bed all year round, were again present. Within two weeks, blue-greens, diatoms, and desmids were evident. After two to four weeks, mosses and liverworts appeared and a thick vegetational mat was present in the stream. Associated with the appearance of the mat was the appearance of carnivorous *Cheumatopsyche* (caddisfly) and *Centroptiloides* (mayfly). After two to three months the vegetation matured and several species of invertebrates were added to the benthos. Hynes concluded that oviposition was the most important source of recolonizing organisms in intermittent tropical streams.

Harrison (1966) also studied an intermittent African stream, this one in Rhodesia. He presented detailed results of the recolonization of two pools and two runs. The pools were sampled ten days after flow resumed. In one pool where the substratum had been baked to dry dust, the early colonizers were the oligochaete *Limnodrilus hofmeisteri*, nematodes, the copepod *Cyclops*, and *Chironomus satchelli*. After nine more days, permanent stream species such as the mayflies *Cloen* and Libellulidae appeared. After about 2½ months, the fauna was indistinguishable from that of permanent streams in the area.

The other pool reported on still had a damp substratum just prior to the onset of flow. After flow resumed, recolonization followed a pattern similar to the one reported above, except that insect larvae were more diverse during the first 10 days. These additional larvae included the chironomid *Procladius*. Harrison states that "normal" faunal composition was established within a month and a half.

Samples taken from one of the runs showed that early colonizers (after one week of flow) included nematodes, oligochaetes, *Cyclops*, large numbers of *Chironomus satchelli*, *Simulium ruficornis*, and Orthocladiinae (chironomids). Baetid mayflies and *Cheumatopsyche* (caddisfly) appeared between the third and sixth week. In the other run studied, the overall recolonization pattern was similar and the fauna returned to approximately normal composition after nine weeks. Harrison found that the recolonizing organisms came from the following sources: gastropods and many oligochaetes from aestivation;

other oligochaetes, small crustaceans and rhabdocoels from resting eggs; and most insects from oviposition after flow was resumed.

Experimental streams. Patrick (1959) reported on the colonization of a newly formed stream in Pennsylvania. The stream bed, made for the purposes of the colonization experiment, was constructed using a bulldozer and backhoe, and water from Ridley Creek was diverted into the channel.

In general, Patrick found that organisms with shorter life spans (e.g., bacteria) were the quickest to establish natural and normal populations. Dipterid insect larvae capable of suspension feeding were the first macrobenthos to invade and become established in the new environment. The snail *Physa* seemed to be the best established invertebrate after six months. The general lack of establishment after six months of many important invertebrates otherwise occurring in the parent stream led Patrick to conclude that the pattern of colonization seemed to be more influenced by organism life history and environmental factors than by random drift downstream from upstream habitats.

Recolonization of stream bottoms after pollution abatement. There is extensive literature concerning the effects of pollutants on individual species and communities inhabiting streams, but only a few of these studies give detailed documentation of the biological recovery process following a pollution event. Cairns et al. (1971) found that the rate of the recovery process is dependent on the distance of the affected portion of the river from the pollution source and the presence of undamaged tributaries. The nature of the disturbance—long-term versus short-term—is also important in this respect, as is the degree of residual toxicity.

But while the rate of recovery is variable, the taxonomic pattern of recovery is much more predictable. For example, Brinkhurst (1965) showed that the usual inhabitants of a polluted stream (particularly a stream affected by organic pollution) occurred in low-diversity, oligochaete-dominated communities. Brinkhurst further demonstrated that these communities change in a predictable fashion. As pollution is swept away, organisms like chironomids and certain amphipod species become more important as oligochaetes decline. Further improvement in water quality then leads to the establishment of a progressively more diverse community. Crisp and Gledhill (1970), who also studied the recovery of an English stream—a reach of a mill stream that was polluted, then drained and dredged—reported that chironomids were the most abundant early colonizers of the newly reflooded stream. Within a year, molluscs and oligochaetes also became numerically important. Crisp (1970) later performed a related study on a newly formed watercress bed and found a similar taxonomic pattern of colonization.

Standing Water

Natural Lakes

There are few published studies concerning benthic recolonization in natural lakes. A study by Moon (1935) is relevant but was not focused on the subject of colonization. Moon used trays of defaunated (but not deflorated) native sediment to sample the benthos of Lake Windermere, England. After his trays were down four weeks, the fauna on the trays was approximately similar to the fauna on the natural bottom. When the trays were left for longer than four weeks, Moon found very little if any increase in the collected fauna. *Limnaea peregra* (gastropod) and *Gammarus pulex* (amphipod) were numerically dominant early colonizers. Other colonizers included insect larvae, isopods, and leeches. Moon also contended that the trays were not generally suitable for collecting oligochaetes and pisidiid bivalves. Nevertheless, these organisms still showed up on the trays, indicating their abilities as colonizers.

Man-made Lakes

Most man-made lakes are formed by the damming of a river. During the process of lake formation there is a great alteration of both the physical and biological characteristics of the submerged environment. These changes include a continual increase in new habitat until the lake is filled, the concomitant drowning of the associated terrestrial biome and soil, and an overall reduction in current flow. The result is the disappearance of the obligate lotic benthos, the introduction of new species, and the redistribution of surviving lotic forms.

Temperate regions. A general model describing the colonization patterns and processes in temperate reservoirs was put forth by Morduchai-Boltovskoi (1961). According to this model, the colonization sequence may be divided into four stages. During the first stage, lasting only a few months, the benthos is dominated by forms derived from the impounded river. In the second stage, after the river fauna declines, explosive population growth of (usually) a single species of chironomid occurs, often *Chironomus plumosus*. This stage may last up to two or more years and is generally associated with the filling of the reservoir. In the third phase, which often corresponds to early post-filling time, the *C. plumosus* populations decline and are replaced by a more diverse association of chironomids, oligochaetes, and molluscs. The fourth phase begins when faunal equilibrium (stability) is achieved.

This summary viewpoint has received extensive substantiation. For example, Zhadin and Gerd (1961) provided an extensive review of the biology of reservoirs in the Soviet Union (for Polish reservoirs cf. Krzyżanek 1970). Their description of reservoir colonization is largely congruent with the Morduchai-Boltovskoi model: rising

water levels caused by the damming of the river inundate soil and vegetation. Oxidation of materials in the soil and decaying terrestrial vegetation produce low oxygen levels in the water. The relative immobility of the water and low oxygen levels quickly kill off most of the rheophilic forms.

The most conspicuous early colonizer of newly flooded areas (in the first one to two years, say) is larval *plumosus*, which may occur in population densities in the tens of thousands m^{-2} . These populations apparently are supported by the abundant organic detritus. Later, *C. plumosus* populations decline and are in part replaced by a less abundant but more diverse bottom fauna. These remaining forms may often be actively burrowing forms like tubificid oligochaetes and glyptotendiped chironomids. An exception to this pattern occurs on relief patches of silty and sandy river bottom. Here benthic diversity is generally higher through the filling phase, perhaps in part due to the presence of plants and large rocks.

Besides chironomids, other important early colonizers on the newly flooded soils often include amphipods and mysids (crustaceans). Molluscs, and particularly oligochaetes, may rise to dominance after the chironomids decline. In general, the overall taxonomic pattern of colonization of the inundated soils in these reservoirs shows a short-lived pioneer chironomid community followed after about two years by a more stable and diverse oligochaete community.

Paterson and Fernando (1969) also provided substantiating information for the Morduchai-Boltovskoi model from a Canadian impoundment, Laurel Creek Reservoir. Their illustrations are instructive and two are reproduced here. Figure 1 shows the explosive growth of chironomid populations during the first year of the reservoir's existence. Figure 2 depicts the pattern of population growth of other early colonizers. Note particularly the relatively more stable growth of oligochaete populations compared to chironomid populations.

Several studies have provided additional resolution of the colonizing process in temperate reservoirs. Nursall (1952), for example, was able to recognize a successional pattern involving the pioneer chironomid community during the first two years of existence of the Barrier Reservoir, Alberta. This succession, *Pentapedilum* to *Chironomus* to *Tanytarsus*, appeared to be related to changes in the organic content of the sediments. Nursall thought that the bottom and the reservoir as a whole changed from eutrophic to oligotrophic as the leaf litter of the original bottom became covered by sediments. McLachlan and Cantrell (1976) provided additional evidence of the relationship between substratum properties and the colonizing process. In newly formed Ladyburn Lough, they found the distribution of the early colonizer *C. plumosus* in part determined by substratum type: it selectively colonized muddy sediments and avoided the harder erosional areas. Similarly, sediment depth determined the shape of its larval tube.

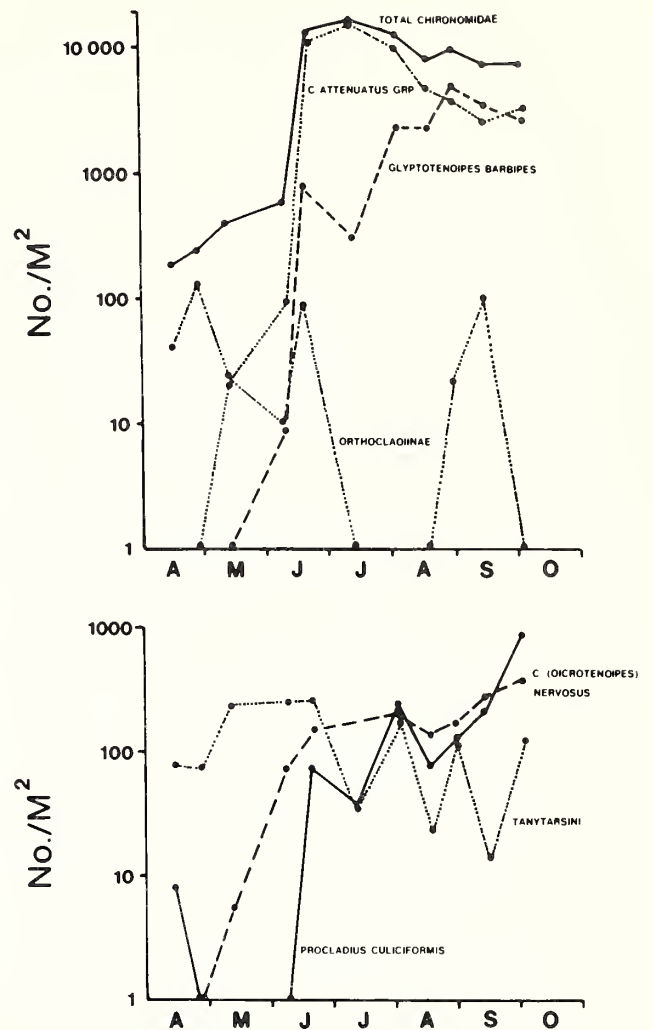


Fig. 1. Growth of chironomid populations in Laurel Creek Reservoir (redrawn from Paterson and Fernando 1969).

The overall taxonomic pattern of colonization of Barrier Reservoir is illustrated in Figure 3. It is interesting to note that oligochaetes are more abundant than some of the chironomids in the very early history of the reservoir. Armitage (1977) also showed that oligochaetes along with chironomids are important early colonizers in some English impoundments.

Other artificially formed lentic habitats show benthic colonization patterns that are similar to those of temperate reservoirs. For example, McLachlan (1975a) reported on the colonization of a series of basins in northeast England which resulted from abandoned mining operations and which were filled by diverting a stream. The initial substratum of these basins consisted of boulder-clay subsoil. McLachlan was especially concerned with monitoring the invertebrate colonization of the water-filled basins, and relating the patterns of colonization to the degree of isolation of certain basins from the adjacent

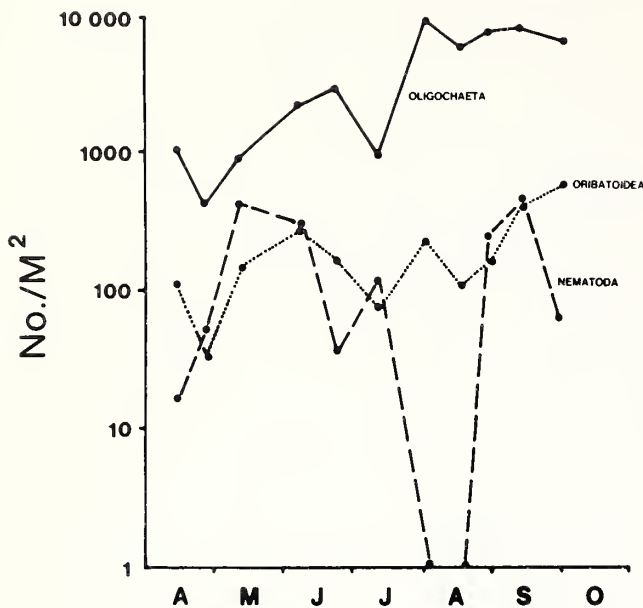


Fig. 2. Macroinvertebrate colonization of Laurel Creek Reservoir (redrawn from Paterson and Fernando 1969).

stream fauna, and also the time of year when the colonization began. Most of his colonization data were collected over a 23-month period. His main conclusions were as follows: the important summer colonizer was the *Chironomus plumosus* group, which built up large populations within a few months as a result of oviposition. The predominant winter colonizer was also a chironomid, *Procladius choreus*, which invaded new areas by larval migration. McLachlan stated that this mode of colonization was slower than oviposition and only occurred when the colonized pools were in direct contact with an established fauna. Therefore, colonization of isolated pools did not take place in the winter because oviposition did not take place. But in either case, the monospecific chironomid assemblages were replaced by more diverse mollusc-oligochaete communities.

The colonization sequence in reservoirs has parallels in several lentic habitats, so long as they are influenced by some form of disturbance. For example, Hynes (1961) studied the effects of artificially induced water level fluctuations on the littoral fauna of Lake Bala, Wales. This form of disturbance greatly reduced the diversity and abundance of the former littoral fauna. But these forms were replaced by two species of oligochaetes (*Stylo-drilus vej dovskyi* and *?Henlea* sp.) that became extremely abundant. *Pelescolex* (oligochaete) and several chironomids that previously occurred in the sublittoral also came to occupy the littoral zone.

Kaser and Jacobi (1978) also demonstrated rapid (≈ 3 months) recolonization by chironomids and oligochaetes in draw-down areas in a Wisconsin reservoir. Driver (1977) similarly talked about fluctuating water levels adversely affecting chironomid species richness in small prairie ponds in central Saskatchewan.

Gersbacher (1937) performed related studies when he investigated community development in large artificial pools in Illinois streams and community structure at various stream habitats (e.g., source, mouth, tributaries, different flow regimes). He found that the first stage in the colonization sequence in pools was the development of the *Chironomus plumosus* community. Typically, fairly large numbers of *plumosus* ($10 \text{ s}'/\text{m}^2$) developed within a few months after the pools formed. Shallower water was occupied first, then several months later deeper water began to be inhabited. Increased deposition of both organic and inorganic sediments and the increased presence of plankton in the pools, in Gersbacher's opinion, prepared the way for further succession.

Between 5 to 10 years later, *C. plumosus* populations declined and *Procladius* increased in numbers, and *Hexagenia* (mayfly nymph) and *Musculium* (pisiid bivalve) also appeared. This heralded the onset of the *Hexagenia-Musculium* community, whose other components included freshwater mussels and the oligochaete *Limnodrilus*. The composition of this community varied, depending on local current and substratum conditions. For example, *Hexagenia* and *Limnodrilus* were generally absent where current flow was rapid. But where extensive siltation occurred in quiet waters, *Limnodrilus* and ceratopogonids predominated. Many predatory fishes characterized this second stage of community development.

Gersbacher emphasized the role of disturbance in shaping communities. He reported, from his longitudinal survey of the stream, that habitats prone to drying and flooding have earlier-stage communities than less disturbed areas. Also, sand bottoms, because of their instability, have poorly developed faunas. Gersbacher concluded that the overall relationship between substratum distribution, disturbance, and community development within the stream has parallels in terms of community succession in the pools.

Tropical regions. Much of the literature on benthic colonization of man-made tropical lakes concerns African reservoirs. Although the subject of macroinvertebrate colonization of these African reservoirs has received an excellent review (McLachlan 1974a), some of the main points of that review are summarized in order to better develop and clarify comparisons of macroinvertebrate colonization in diverse freshwater situations.

According to McLachlan (1974a; see also his references), the filling phase of the newly forming reservoir has distinctive physical and chemical characteristics which include high turbidity and an irregular shoreline (both due to the rising waters), low levels of dissolved oxygen and high dissolved salt content (both due to decomposing organic debris of terrestrial origin), and high organic content (derived from terrestrial biome). Correlated with these physical and chemical factors is an explosive population growth of a few species of invertebrates, notably chironomids, copepods, and cladocerans. Other organ-

Nursall: Fauna

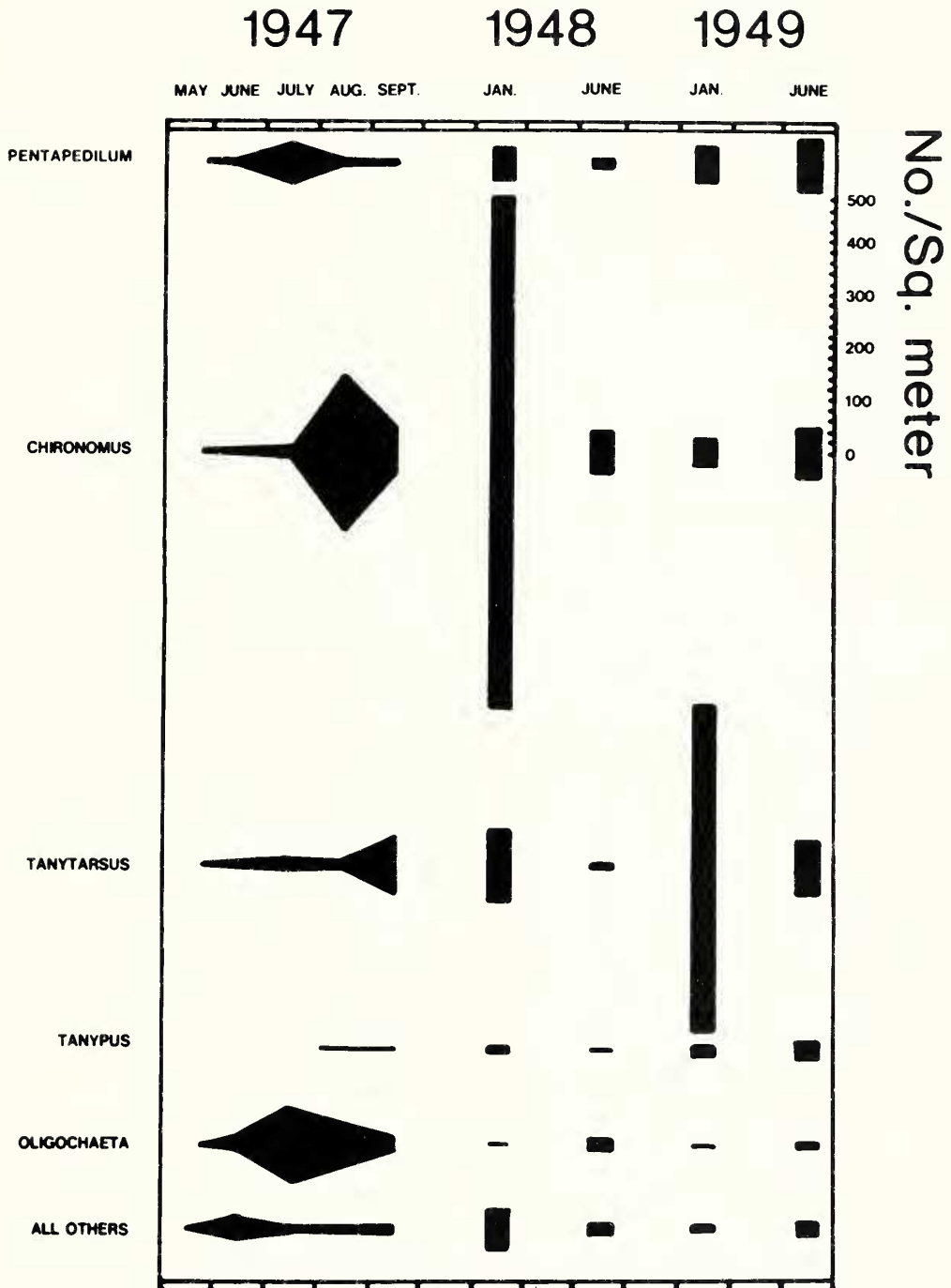


Fig. 3. Macroinvertebrate colonization of Barrier Reservoir (redrawn from Nursall 1952).

isms that show large increases in numbers include blue-greens, floating plants, and fish.

Among the invertebrates, the dynamics of chironomid colonization has been most extensively studied. Chironomid larvae are the most prominent of the early benthic colonizers, and chironomid communities often persist through the colonization cycle. Chironomid colonization of tropical impoundments generally follows a consistent pattern: shallow water is colonized first, usually by one highly abundant species. For example, Petr (1971) observed that a bottom flooded for 25 days in Lake Volta, Africa, contained chironomid population densities of 800m⁻². Over the course of several months to a few years, this community is replaced by one composed of several species and lower abundance.

The presence of submerged woodland and floating plants can alter the nature of the colonization cycle which is chironomid-dominated on soft bottoms. Drowned forests provide a suitable substratum for the wood-boring mayfly *Povilla*; thus a *Povilla*-dominated community may succeed the pioneer chironomid community during the filling phase if suitable substrata are available. Also, McLachlan (1975b) pointed out that the presence of aquatic macrophytes generally promotes faunal diversity in tropical lakes.

The post-filling phase, according to McLachlan (1974a) is characterized by the reduction of allochthonous materials entering the lake. Nutrients for plant growth mainly come from the decomposition of materials drowned during the filling phase. Compared to that phase, dissolved oxygen levels increase, turbidity decreases, and organic influx is less in the post-filling phase.

McLachlan (1974a) explains why fluctuations in lake level are important in affecting successional patterns during the post-filling phase. On soft substrata, grass may grow on exposed lake margins when the lake level temporarily drops. Dung then accumulates in this area from herbivores that eat the grass during low-stand of the lake. When lake level rises, this nutrient-enriched substratum usually is inhabited by a single species of chironomid larva that occurs in large numbers. Prior to the fall of lake level and without this enrichment, a more diverse chironomid community would inhabit this area (cf. Marshall 1978).

Petr (1971, 1974) showed that the species composition of chironomid communities in tropical reservoirs was also strongly affected by substratum properties. Genera such as *Chironomus*, *Nilodorum*, and *Dicrotendipes* are usually associated with organic-rich muddy substratum. Many tanytarsini, on the other hand, prefer sandy substrata. Substratum changes in an impoundment may occur during the post-filling phase by exposing areas of the bottom to increased wave activity. For instance, Petr (1971) points out that the gradual destruction of belts of flooded trees that protect shallow water would result in

increased wave action transporting away the fine component of the substratum. McLachlan and McLachlan (1976) also showed that the distribution of the mud substratum affected the distribution of certain colonizing organisms.

One other potentially important factor in affecting the colonizing process—biotic interactions—has received comparatively little attention. Cantrell and McLachlan (1977) demonstrate from laboratory evidence that the distribution of major species of chironomids in a newly flooded lake may be the result of competitive interactions. They concluded that the activities of *C. plumosus* larvae cause *Tanytarsus gregarius* larvae to move to areas of the lake where interspecific encounters are less frequent (e.g., lake margins). The relative size of the competing larvae (*C. plumosus* being in general the largest) was considered to be the critical factor in the competition for space.

Concerning the final or equilibrium phase of tropical reservoirs, McLachlan (1974a) feels that the oldest of the African man-made lakes, Kariba, which finished filling in 1963, may have just at the time of his writing begun entering the equilibrium phase. But as he also points out, the species diversity of the littoral zone of these lakes was still far less than that of permanent tropical lakes.

Recolonization of lentic benthos after pollution abatement. As in the case of streams, rather few studies give details of the recovery of lentic faunas after pollution abatement. A brief summary of one of these detailed studies is presented below.

Lellák (1966) reported on the recovery of the bottom fauna of five Elbe backwaters following poisoning that removed almost all fish and killed most of the benthos. Lellák found that chironomid larvae, including *C. plumosus*, were the dominant early colonizers. Chironomids then declined after a few months and were replaced by a benthic fauna dominated by tubificid oligochaetes. After approximately one year, the oligochaetes declined, and organism abundance and species richness stabilized. Lellák also noted a temporal replacement of trophic groups, with surface-feeding or suspension-feeding forms being replaced by groups that feed at deeper levels within the sediment.

Temporary Lentic Environments

Temporary ponds. Kenk (1949) studied invertebrate succession in two temporary ponds in Michigan and observed the following stages of invertebrate recolonization within them: In the first stage ("winter stage," beginning November-December) the ponds were filled by rainwater after summer drying. Ostracods (crustaceans) and copepods were conspicuous early colonizers, with some species appearing within 1½ days of the first standing water. Other colonizers that appeared within about two weeks included chironomids and gastropods. Overall, the spe-

cies richness of this stage was relatively low (<70 species). The flatworm *Phagocata vernalis* was the dominant form, and other important organisms included small crustaceans, diptera larvae, pisidiid bivalves, and the gastropod *Gyraulus*.

The second stage ("spring stage," beginning March-April) began when the ice melted and the ponds began to warm up. *Phagocata* populations quickly declined and were replaced by those of another flatworm, *Dalyellia*. The most characteristic species of the early spring was the fairy shrimp *Eubranchipus*. Populations of clam shrimps (*Lynceus*) also appeared in the early spring and persisted until the ponds dried up in late June or July. *Eubranchipus*, however, disappeared from the ponds before the summer dry period. After *Eubranchipus* disappeared, *Lynceus* reached maximum abundance. As the spring stage progressed, numerous predators appeared. These included coleoptera (beetle) larvae, Odonata nymphs, and Hemiptera (true bugs). Naidid oligochaetes were also present at this time. In all, about 200 species of invertebrates appeared in the pond during the spring stage.

The final stage of the cycle comprised the ponds undergoing summer drying and remaining so until the onset of late autumn rains.

The earliest colonizers and many of the winter stage species (e.g., ostracods, copepods, flatworms) recolonized the pond via eggs or resting stages which had survived desiccation, according to Kenk (1949) Phyllopod crustaceans, conspicuous in the early spring stage, also emerged from eggs. In contrast, many of the insect predators that characterized the later part of the spring stage either migrated in at that time as adults or hatched from rapidly developing eggs that had been laid by flying adults earlier in the spring.

Kenk (1949) suggested that predation and substratum modification by organisms may influence the colonization cycle. Concerning the former, he said that the disappearance of fairy shrimp may be related to the appearance of fish and predaceous insects. Concerning the importance of biogenic sediment alteration, he pointed out that crayfish burrows first provide a moist refugia in which several species of pond organisms reside when the ponds dry up, and then they represent an important conduit for colonizing organisms when the ponds refill.

Tropical rainpools. Rzoska (1961) studied the colonization or tropical rainpools in the vicinity of Khartoum, Sudan. He found that important pool organisms included phyllopods, copepods, cladocerans, and rotifers. Ciliates, nematodes, insect larvae, ostracods, and adult Hemiptera were minor constituents of the fauna. The recolonization of the pools proceeded as follows: *Moina* and *Metacyclops* (copepods) were important early colonizers and appeared in abundance within four days after the pools formed. Rotifers became numerous as early as the fifth

day. Also by the fifth day, large conchostracans appeared. Other crustaceans became important later. By the tenth day phyllopods were abundant, and by the fourteenth day *Triops* had appeared.

Rzoska (1961) observed that all the forms examined in the pools were characterized by very rapid growth, early maturation (within a few days of hatching), and extremely high fecundity. All the organisms in the pools apparently originated from resting stages in the soil (eggs or cysts). Algal growth was not visible in the pools.

Tropical lakes. McLachlan (1974b, 1975b) studied the recolonization of Lake Chilwa in tropical Africa, after it refilled following drying. He found that the dominant early colonizer was larval *Chironomus transvaalensis*. After six weeks of filling, its population had reached 3,500 mg/m. After twelve weeks it had virtually disappeared, leaving behind a scanty benthos. He also found (1975b) that vegetation played an important role in the recovery of the lake. For example, only 11 species of benthic organisms were found on the mud substratum of the lake, while 40 were found on the vegetation. Furthermore, the floating plants hosted a greater variety of species than emergent plants, because the floating species are not alternately stranded, then reflooded, during water-level changes.

A similar colonization pattern (or aspects of it) also obtains for annual storage reservoirs (McLachlan 1974a; also cf. Bay et al. 1966, for a temperate analog) and areas of lakes subject to periodic emergence due to fluctuating water levels (e.g., Lake Mcllwaine, Rhodesia; see Marshall 1978).

Results

It is possible to recognize a small number of taxonomic and functional themes common to many of the colonization sequences described in the preceding sections. Further, it is possible to relate these themes to the proximity of disturbance as seen in Table 1 which shows taxonomic and functional aspects of some of the more completely described colonization sequences that were previously summarized. The table reveals taxonomic and functional themes common to many different environments. The relation of these themes to disturbance provides clues to understanding the composition and dynamics of freshwater benthic communities.

Taxonomic Themes

A common taxonomic theme of the colonization process in diverse freshwater habitats (e.g., reservoirs, permanent and intermittent streams, pools, and backwaters) consists of a species-poor chironomid community (often a monospecific assemblage of *C. plumosus*) that is eventu-

TABLE 1
Benthic Colonization in Fresh Water

<i>Environment</i>	<i>Disturbance</i>	<i>Typical Early Colonizers</i>	<i>Typical Later Colonizers</i>	<i>Functional Response*</i>	<i>Reference</i>
Permanent stream	Defaunation of native substratum	chironomids	oligochaetes gastropods	1, 2, 3	Tevesz (1978)
Canal	Implantation of artificial substrate	chironomids	gastropods trichopterans Odonata nymphs oligochaetes	1, 2, 3, 4	Cover and Harrell (1978)
Intermittent stream (temperate)	Seasonal drying	chironomids	ephemeropterans crayfish	1, 2, 3, 4	Larimore et al. (1959)
Intermittent stream (tropical)	Seasonal drying	Earliest: cladocerans ostracods Early: chironomids ephemeropterans <i>Simulium</i>	trichopterans ephemeropterans	1, 3	Hynes (1975)
Experimental stream	Creating new stream bed	dipterid insect larvae	gastropods	1, 2, 3	Patrick (1959)
Mill stream	Pollution Draining Dredging	chironomids	molluscs oligochaetes	1, 2, 3	Crisp and Gledhill (1970)
Reservoirs (temperate)	Drowning landscape	chironomids crustaceans	molluscs oligochaetes	1, 2, 3	Zhadin and Gerd (1961)
Reservoirs (temperate)	Drowning landscape	oligochaetes chironomids	oligochaetes chironomids	1, 3	Nursall (1952)
Artificial pools in rivers	Destroying riverine conditions	chironomids	oligochaetes ephemeropterans bivalves	1, 2, 3	Gersbacher (1937)
Reservoirs (tropical)	Drowning landscape	chironomids cladocerans copolods	oligochaetes ephemeropterans	1, 3	McLachlan (1974a)
Backwaters	Poisoning	chironomids	oligochaetes	1, 3	Lellák (1966)
Temporary ponds	Seasonal drying	flatworms chironomids small crustaceans	larger crustaceans beetle larvae Odonata nymphs	1, 2, 4	Kenk (1949)

*Key to Functional Response: 1 — Species richness low → high.

2 — Later colonizers typically larger, less abundant, and better protected than early colonizers.

3 — Early colonizers highly mobile.

4 — Predators appear late in colonization sequence.

ally replaced, in a few months to a few years, by a more species-rich community frequently dominated by oligochaetes, and sometimes molluscs. A second, but less well-defined taxonomic theme may be recognized, primarily in temporary pools. Here, early colonizers are frequently flatworms, small crustaceans, and chironomids. The later colonizers, in contrast, include larger crustaceans, beetle larvae, and occasionally Odonata nymphs.

Both of these kinds of colonization sequences are initiated by diverse forms of disturbance that are responsible for either no fauna or only a depauperate fauna to be present initially. The taxonomic composition of the communities then develops over an increasing distance in time from the disturbance. A relationship between tem-

poral proximity to disturbance and taxonomic composition of these freshwater communities is therefore obvious. Species-poor chironomid communities, for example, appear to be correlated with temporal proximity to disturbance. Contrastingly, species-rich oligochaete/mollusc communities appear to be correlated with a greater temporal distance from disturbance.

Functional Themes

The data in Table 1 also reveal that at least three functional attributes are consistently present in many colonization sequences in these diverse freshwater settings. First, there is the consistent and obvious increase in spe-

cies richness over the colonization sequence. Secondly, later colonizers, irrespective of their taxonomic nature, often appear to be larger and better protected forms than early colonizers (e.g., molluscs versus chironomids). Third, the early colonizers are often highly mobile forms and the recolonization process may be initiated by a reproductive event (e.g., chironomids are noted for their high powers of dispersal because the adult stage is winged; also, larval forms are prone to drifting in streams). Later colonizers are usually not as mobile (e.g., bivalves and gastropods).

Because there are recurrent functional patterns characteristic of these colonization sequences, functional aspects of freshwater communities, like taxonomic aspects, may be correlated with the proximity to disturbance.

Discussion

McCall (1977) demonstrated that taxonomic and functional aspects of certain marine communities were related to the temporal proximity to disturbance. His approach was experimental. He created artificial disturbances by placing containers of defaunated sediment in the natural bottom, then monitored their colonization by benthic macroinvertebrates. His findings concerning the importance of disturbance in the structure and dynamics of marine communities were in contrast to the findings of many previous workers who placed great importance on the controlling influence of ambient physical/chemical environmental parameters.

The findings of this study suggest that disturbance is an important controlling factor in freshwater environments as well. Natural disturbance (e.g., seasonal drying) and artificial disturbances (reservoir filling; the planting of artificial substrata) change the physical and chemical nature of the environment in disparate ways; yet the taxonomic and functional response of organisms communities to disturbance, whatever its nature or wherever it occurs (e.g., in rivers, lakes, reservoirs, or rainpools) appears to be highly predictable. As in the case of marine ecosystems, it seems that community structure and dynamics are closely related to the temporal proximity to disturbance.

Knowing this predictable response to disturbance by invertebrates in aquatic systems likely has practical value. Because pollution is a form of disturbance in aquatic ecosystems, further refinement of the colonization model would probably be of use in gauging the resiliency of particular ecosystems and evaluating the impact of pollution and timing of community recovery from pollution events.

Other environmental factors that are correlated with macrobenthic succession in fresh water include the development of plant communities, the availability of organic detritus, physical and chemical modification of the substratum (sometimes by organisms), and biotic interactions such as predation and competition. Nevertheless,

there is little information available on these subjects in terms of the nature of their relationship to the colonization process.

Suggestions for Further Study

Although the taxonomic details of early succession are fairly well understood, particularly in terms of the chironomids, corresponding details of the later oligochaete-dominant stages are lacking. At best, we are told that some of the later colonizers are "tubificids," although usually they are simply listed as "oligochaetes." Moreover, this chironomid-oligochaete succession, although common, is likely not the whole taxonomic picture. We need more detailed work on interesting exceptions (e.g., Nurnsall 1952).

A complementary functional view of the later stages of succession is also needed. While we know what the low-diversity chironomid communities "look like" and have some idea of what they "do," we lack comparable information on the higher-diversity communities that follow them. Among other things, we need to know what these organisms are feeding on, where they are living within the habitat (e.g., precise substratum level), what they are doing to the physical and chemical properties of the bottom, and how they are interacting with each other.

We also suffer from a lack of knowledge concerning certain environments. For instance, while we know much about colonization in such man-made environments as reservoirs, we know comparatively little about colonization of native substrata in rivers and lakes.

Acknowledgments

F. M. Soster critically reviewed the manuscript and provided helpful suggestions. Drafting was done by M. Ludwig.

References

- Armitage, P. D. 1977. Development of the macro-invertebrate fauna of Cow Green Reservoir (Upper Teesdale) in the first five years of its existence. *Freshwater Biology* 7:441-454.
- Bay, E. C., A. A. Ingram, and L. D. Anderson. 1966. Physical factors influencing chironomid infestation of water-spreading basins. *Annals of the Entomological Society of America* 59:714-717.
- Brinkhurst, R. O. 1965. Observations on the recovery of a British river from gross organic pollution. *Hydrobiologia* 25:9-51.
- Cairns, J., J. S. Crossman, K. L. Dickson, and E. E. Herricks. 1971. The recovery of damaged streams. *Association of South-eastern Biologists, Inc., Bulletin* 18:79-106.
- Cantrell, M. S., and A. J. McLachlan. 1977. Competition and chironomid distribution patterns in a newly flooded lake. *Oikos* 29:429-433.
- Clifford, H. F. 1966. The ecology of invertebrates in an intermit-

- tent stream. *Investigations of Indiana Lakes and Streams* 7:57-98.
- Cover, E. C., and R. C. Harrel. 1978. Sequence of eolonization diversity, biomass and productivity of macroinvertebrates on artificial substrates in a freshwater canal. *Hydrobiologia* 59:81-95.
- Crisp, D. T. 1970. Input and output of minerals for a small watercress bed fed by chalk water. *Journal of Applied Ecology* 7:117-139.
- Crisp, D. T., and T. Gledhill. 1970. A quantitative description of the recovery of the bottom fauna in a muddy reach of a mill stream in southern England after draining and dredging. *Archiv für Hydrobiologie* 67:502-541.
- Driver, E. A. 1977. Chironomid communities in small prairie ponds: Some characteristics and controls. *Freshwater Biology* 7:121-133.
- Gersbacher, W. M. 1937. Development of stream bottom communities in Illinois. *Ecology* 18:359-390.
- Glime, J. M., and R. M. Clemons. 1972. Species diversity of stream insects on *Fontinalis* spp. compared to diversity on artificial substrates. *Ecology* 53:458-463.
- Harrison, A. D. 1966. Recolonization of a Rhodesian stream after drought. *Archiv für Hydrobiologie* 62:405-421.
- Hynes, H. B. N. 1961. The effect of water level fluctuations on littoral fauna. *Verhandlungen der Vereinigung Internationalen für Theoretische und Angewandte Limnologie* 14:652-656.
- Hynes, J. D. 1975. Annual cycles of macro-invertebrates of a river in southern Ghana. *Freshwater Biology* 5:71-83.
- Kaster, J. L., and G. Z. Jacobi. 1978. Benthic macroinvertebrates in a fluctuating reservoir. *Freshwater Biology* 8:283-290.
- Kenk, R. 1949. The animal life of temporary and permanent ponds in southern Michigan. *Miscellaneous Publications of the Museum of Zoology of the University of Michigan* 71:1-66.
- Krzyżanek, E. 1970. Formation of Bottom Fauna in the Goczałkowice Dam Reservoir. *Acta Hydrobiologica* 12:399-421.
- Larimore, R. W., W. F. Childers, and C. H. Rotte. 1959. Destruction and reestablishment of stream fish and invertebrates affected by drought. *Transactions of the American Fisheries Society* 88:261-285.
- Lellák, J. 1966. Influence of the removal of the fish population on the bottom animals of the five Elbe backwaters. In J. Hrbacek, ed., *Hydrobiological Studies*, 1:323-380. Prague, Czechoslovakia: Academia Publishing House.
- Marshall, B. E. 1978. Aspects of the ecology of benthic fauna in Lake McIlwaine, Rhodesia. *Freshwater Biology* 8:241-249.
- Mason, W. T., J. B. Anderson, R. D. Kreis, and W. C. Johnson. 1970. Artificial substrate sampling, macroinvertebrates in a polluted reach of Klamath River, Oregon. *Journal-Water Pollution Control Federation* 42:R315-R328.
- McCall, P. L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. *Journal of Marine Research* 35:221-266.
- McLachlan, A. J. 1974a. Development of some lake ecosystems in tropical Africa, with special reference to the invertebrates. *Biological Reviews of the Cambridge Philosophical Society* 49:365-397.
- . 1974b. Recovery of the mud substrate and its associated fauna following a dry phase in a tropical lake. *Limnology and Oceanography* 19:74-83.
- . 1975a. The development of chironomid communities in a new temperate impoundment. *Entomologisk Tidskrift* 95, Suppl., 162-171.
- . 1975b. The role of aquatic macrophytes in the recovery of the benthic fauna of a tropical lake after a dry phase. *Limnology and Oceanography* 20:54-63.
- McLachlan, A. J., and M. A. Cantrell. 1976. Sediment development and its influence on the distribution and tube structure of *Chironomus plumosus* L. (Chironomidae, Diptera) in a new impoundment. *Freshwater Biology* 6:437-443.
- McLachlan, A. J., and S. M. McLachlan. 1976. Development of the mud habitat during the filling of two new lakes. *Freshwater Biology* 6:59-67.
- Moon, H. P. 1935. Methods and apparatus suitable for an investigation of the littoral region of oligotrophic lakes. *Internationale Revue Gesamten Hydrobiologie und Hydrographie* 32:319-333.
- Morduchai-Boltovskoi, F. D. 1961. Die Entwicklung der Bodenfauna in den Stauseen der Wolga. *Verhandlungen der Vereinigung Internationalen für Theoretische und Angewandte Limnologie* 14:647-651.
- Nursall, J. R. 1952. The early development of a bottom fauna in a new power reservoir in the Rocky Mountains of Alberta. *Canadian Journal of Zoology* 30:387-409.
- Paterson, C. G., and C. H. Fernando. 1969. The macroinvertebrate colonization of a small reservoir in eastern Canada. *Verhandlungen der Vereinigung Internationalen für Theoretische und Angewandte Limnologie* 17:126-136.
- Patrick, R. 1959. Aquatic life in a new stream. *Water and Sewage Works*, December, 531-535.
- Petr, T. 1971. Establishment of chironomids in a large tropical man-made lake. *Canadian Entomologist* 103:380-385.
- . 1974. Dynamics of benthic invertebrates in a tropical man-made lake (Volta Lake 1964-1968), standing crop and bathymetric distribution. *Archiv für Hydrobiologie* 73:245-265.
- Rhoads, D. C., P. L. McCall, and J. Y. Yingst. 1978. Disturbance and production on the estuarine seafloor. *American Scientist* 66:577-586.
- Rzoska, J. 1961. Observations on tropical rainpools and general remarks on temporary waters. *Hydrobiologia* 17:265-286.
- Stehr, W. C., and J. W. Branson. 1938. An ecological study of an intermittent stream. *Ecology* 19:294-310.
- Tevesz, M. J. S. 1978. Benthic recolonization patterns in the Vermilion River, Ohio. *Kirtlandia* 27. 17 pp.
- Waters, T. F. 1964. Recolonization of denuded stream bottom areas by drift. *Transactions of the American Fisheries Society* 93:311-315.
- Williams, D. D., and H. B. N. Hynes. 1976. The recolonization mechanisms of stream benthos. *Oikos* 27:265-272.
- Zhadin, V. I., and S. V. Gerd 1961. Fauna and flora of the lakes and reservoirs of the U.S.S.R. (Reki, ozera i Vodokhranilishcha SSSR. Ikh fauna i flora. Moskva, 1961) *Israel Program for Scientific Translations*, Jerusalem, 1963, pp. 453-532.